

ACHENE MICRO-MORPHOLOGY AS A SYSTEMATIC
AID TO THE SERIES PLACEMENT OF SVENSON'S
UNDESIGNATED *ELEOCHARIS*
(CYPERACEAE) SPECIES

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ABSTRACT

Eleocharis species unassigned by Svenson to the series level at the completion of his worldwide monograph were examined utilizing scanning electron microscopy. Acid treated achenes with their cuticle and outer periclinal cell walls removed revealed micro-morphological characters in support of assigning *E. squamigera* and *E. subarticulata* to the series *Palustriformes*, subseries *Truncatae*. Although the results failed to delegate unequivocally *E. albida* and *E. melanocarpa*, additional insight regarding their infrageneric relationship was obtained. An assessment of *E. minarum* proved to be impossible due to the absence of mature achenes.

Key Words: Cyperaceae, *Eleocharis*, micro-morphology, SEM, achene

INTRODUCTION

The last monographic study of *Eleocharis* R. Br., on a cosmopolitan basis, was conducted by Svenson (1939a). Svenson (1929, 1939a) partitioned *Eleocharis* at the series and subseries levels, based on macro-morphological characters of the culm, floral scales, and fruit, with the achenes being of particular importance. Of the 146 species recognized by Svenson (1939a), five were left unassigned to the series level (*E. albida* Torr., *E. melanocarpa* Torr., *E. minarum* Boeck., *E. squamigera* Svens. and *E. subarticulata* (Nees) Boeck.). Svenson elected to place these plants under the heading "species of uncertain classification" due to the absence or conflicting distribution of diagnostic characters.

Recent survey papers on the micro-morphology of *Eleocharis* achenes found sufficient epidermal characters to warrant their use taxonomically (Varma et al., 1989; Menapace, 1991). A detailed account of achene micro-characters at the series level is provided by Menapace (1991). Such characters as the configuration of the anticlinal cell walls (e.g., entire, crenate, etc.), the contour of the cell lumens (e.g., level, concave, etc.), and the presence or absence of lumen pits and depressions, were found to be systematically

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helpful at the series and subseries ranks. SEM photomicrographs of achenes of representative species were provided in that paper (Menapace, 1991) to illustrate the characters just enumerated.

Given the undesignated series status of the taxa named above, it was of interest to determine if the micro-morphology of their achene walls would add additional features from which to assess their subgeneric relationship.

MATERIALS AND METHODS

Mature achenes were removed from selected herbarium specimens. In order to evaluate infraspecific variation, two or three collections of each species were examined covering as wide a geographic distribution as possible. Data pertaining to the voucher specimens are provided in Table 1. The cuticle and outer periclinal cell walls of *Eleocharis* achenes obscure systematically pertinent micro-morphological features. As a consequence, these layers must be removed to permit observation of the taxonomically useful characters affiliated with the anticlinal cell walls and cell lumens. The cuticle and outer periclinal cell walls were eliminated by submerging the achenes for 24 hours into a 1:9 concentration of sulfuric acid and acetic anhydride. The achenes were subsequently removed from the acid mixture, sonicated, washed with distilled water, and coated with 30 nm of a gold-palladium alloy utilizing an International Scientific Instruments (ISI) PS2 coating unit. Micrographs were taken solely from the central portion of the achenes with an ISI Alpha-9 Scanning Electron Microscope.

RESULTS AND DISCUSSION

In a prior study of *Eleocharis* (Menapace, 1991), X-ray spectrometry determined that silicon is the prevailing element of the achene wall, the chemical form of which is believed to be silica.

The initial micrograph (Figure 1) presents an *Eleocharis* achene with the cuticle and outer periclinal cell walls intact. All remaining micrographs, with the exception of Figures 2, 3, and 11, are *Eleocharis* achenes in which the cuticle and outer periclinal cell walls have been removed to reveal features of the anticlinal cell walls and cell lumens.

Table 1. Collection data of specimens utilized for SEM observations.

- Eleocharis acicularis*. UNITED STATES. **Illinois**: Jackson Co., Elkville, *Mohlenbrock 5760* (SIU); **Nebraska**: Lincoln Co., Kings Lake, *Kellogg s.n.* (SIU); **Maine**: Knopp Co., Razorville, *Steyermark 712* (MO).
- Eleocharis albida*. BERMUDA. **Pembroke Parish**: Pembroke Marsh, *Moore 3164* (GH); MEXICO. **Tamaulipas**: Tampico, *Palmer 570* (GH); UNITED STATES. **Florida**: Levy Co., Waccasassa Bay, *Easterday s.n.* (FSU).
- Eleocharis elegans*. CUBA. **Oriente**: La Carmit Florida Blanca, *Clements 1990* (GH); ECUADOR. **Guayas**: Tenquel, *Holmgren 99* (S); JAMAICA. **St. Anne**: Frazer, *Proctor 34808* (U).
- Eleocharis elliptica*. UNITED STATES. **Michigan**: Charlevoix Co., Beaver Island, *Menapace, 24* (SIU); Beaver Island, *Menapace 25* (SIU).
- Eleocharis filiculmis*. BELIZE. **Cayo**: San Luis, *Dwyer 338* (SIU); DOMINICAN REPUBLIC. **Trujillo**: Bayaquana, *Alain 22448* (GH); HONDURAS. **Morazan**: Las Mesas, *Williams 17054* (WIS).
- Eleocharis geniculata*. JAMAICA. **Manchester**: Cut River, *Proctor 35384* (U); PERU. **Loreto**: Pongode Manseriche, *Mexia 6174* (GH); UNITED STATES. **Florida**: Gulf Co., White City, *Godfrey 75703* (FSU).
- Eleocharis intermedia*. CANADA. **Ontario**: Renfrow Co., Lyndoch Township, *Dickson 1413* (CAN); UNITED STATES. **Indiana**: Nobel Co., Blackman Lake, *Deam 21865* (IND); **Massachusetts**: Berkshire Co., Pontoosue Lake, *Churchill s.n.* (MO).
- Eleocharis melanocarpa*. UNITED STATES. **Indiana**: Porter Co., Indiana Dunes St. Park, *Umbach 3817* (MO); **Texas**: Leon Co., Oakwood, *Palmer 13404* (MO); **Massachusetts**: Barnstable Co., Osterville, *Proctor 38072* (IR).
- Eleocharis multicaulis*. FRANCE. **Allier**: Chassignol 903 (NY); PORTUGAL. **Azores**: Terceira Island, *Silva 135* (NY); SWEDEN. **Blekinge**: Ronneby, *Broddeson 2* (NY).
- Eleocharis nodulosa*. GUATEMALA. **El Quiche**: Nabaj, *Proctor 25301* (U); HONDURAS. **Comayagua**: Siguatepeque, *Errazuriz 112* (SIU); **Morazan**: La Venta, *Espinosa 168* (SIU).
- Eleocharis pachystyla*. COSTA RICA. **Puntarenas**: *Davidse 1269* (MO); CUBA. **Moa**: Oriente, *Clements 3588* (GH).
- Eleocharis parvula*. UNITED STATES. **Florida**: Collier Co., Marco, *Kattato 749* (SIU).
- Eleocharis quinqueflora*. CANADA. **Saskatchewan**: Cypress Hills, *Breitung 5178* (MO); UNITED STATES. **Illinois**: McHenry Co., Ringwood, *Vassey s.n.* (SIU); **Michigan**: Charlevoix Co., Beaver Island, *Menapace 87* (SIU).
- Eleocharis pellucida*. JAPAN **Honshu**: *Togasi 1103* (NY); Nara City, *Kitagawa 307* (NY); **Kyushu**: Lake Odako, *Koyama 7012* (NY).
- Eleocharis rostellata*. UNITED STATES. **Arizona**: Santa Cruz Co., Canelo Hills Nature Preserve, *Adams s.n.* (SIU); **New Jersey**: Ocean Co., Barnegat Bay, *Hermann 4392* (MO).
- Eleocharis squamigera*. BRAZIL. **Parana**: Jaguariaiva, *Dusen 13276* (NY); **Santa Catarina**: Campo Ere, *Smith 13673* (NY); Cacador, *Smith 8982* (NY).
- Eleocharis subarticulata*. BRAZIL. *Gardner 719* (MO); **Santa Catarina**: Cacador, *Smith 8990* (NY); **Parana**: Curitiba, *Dusen 116a* (NY).
- Eleocharis tenuis*. UNITED STATES. **New Jersey**: Ocean Co., Lanoka Harbor, *Hirt 1387* (NY); Cape May Co., Villas, *Wilson 910* (NY); **New York**: Suffolk Co., *Cambell 163* (GH).

In the discussion that follows the "species of uncertain classification" are assessed in accordance with the micro-morphological characters of the achene wall.

***Eleocharis albida* Torr.**

Eleocharis albida is a North American maritime spikerush from Maryland to central Mexico (Gleason, 1952). In his initial review of *Eleocharis*, Svenson (1929) assigned *E. albida* to the series *Sulcatae*, only to describe it at the completion of his study as a plant of "... unknown affinity . . .," a species not allied to any other *Eleocharis* (Svenson, 1939a). In his final monographic work, covering North American *Eleocharis*, Svenson (1957) suggested that *E. albida* may be allied to the series *Pauciflorae*, although a detailed justification was not provided.

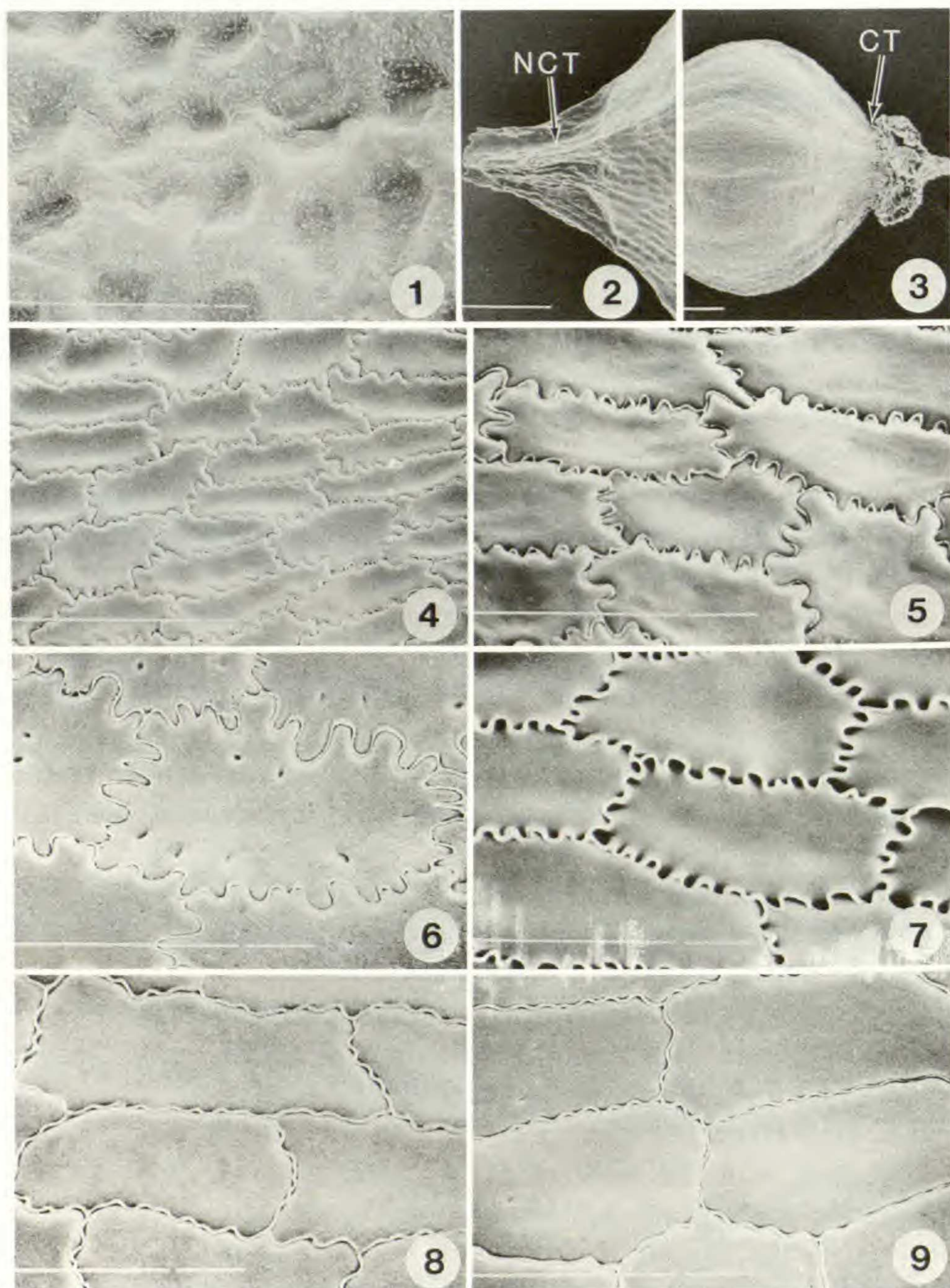
Plants of the *Pauciflorae* possess trigonous achenes that lack a constricted tubercle (e.g., *E. parvula* (R. & S.) Link, Figure 2, NCT). The fruit of *E. albida* is in fact trigonous, however, a large constricted tubercle is also present (Figure 3, CT). There is little question that the constricted condition of the tubercle persuaded Svenson to refrain from formally assigning *E. albida* to the *Pauciflorae*.

On a micro-morphological basis, the achenes of *E. albida* (Figures 4 and 5) bear widely crenate to dentate anticlinal cell walls, with undulating to level lumens that are rarely pitted. Attributes of this nature suggest a relationship with *E. filiculmis* Kunth series *Sulcatae* (Figure 6), *E. multicaulis* (Smith) Smith series *Multicaules* (Figure 7), *E. pellucida* Presl series *Multicaules* (Figure 8), and *E. pachystyla* (Wright) C. B. Clarke series *Sulcatae* (Figure 9).

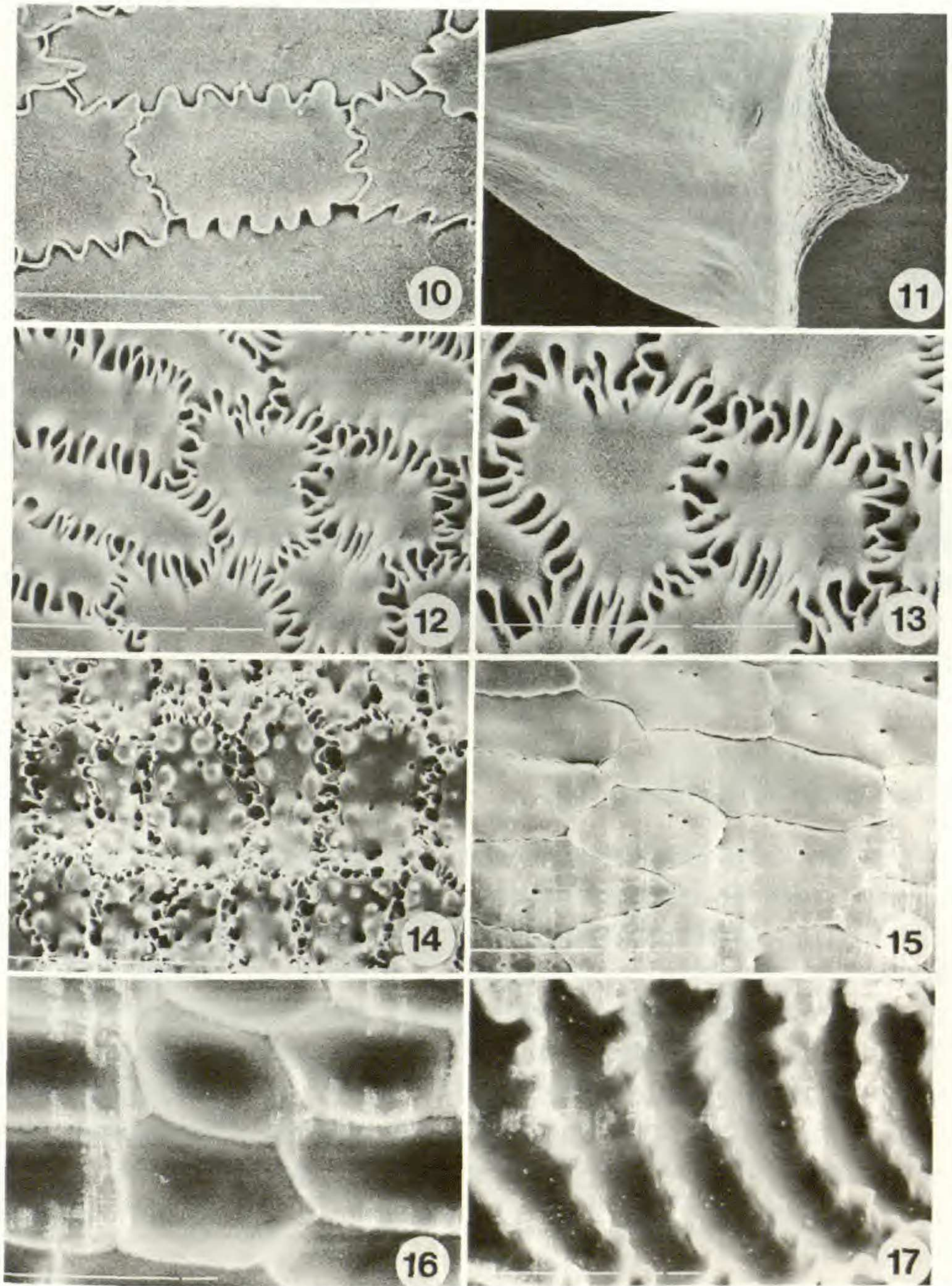
The anticlinal cell walls of *E. geniculata* (L.) R. & S. (Figure 10), series *Maculosae*, are also crenate to dentate. However, in contrast to the trigonous achenes of *E. albida*, the achenes of *E. geniculata* are lenticular. Such a salient difference is sufficient, in the author's judgement, to preclude a close affiliation between *E. geniculata* and *E. albida*.

***Eleocharis melanocarpa* Torr.**

Although encountered sporadically within the interior of North America, *E. melanocarpa* is primarily a sedge of the Atlantic coastal plain from Massachusetts to Texas (Gleason, 1952). Sven-



Figures 1-9. 1. *E. melanocarpa* (Proctor 38072). 2. *E. parvula* (Kattato 749), Bar = 100 μm . 3-5. *E. albida* (Moore 3164), Bar = 100 μm . 6. *E. filiculmis* (Williams 17054). 7. *E. multicaulis* (Silva 135). 8. *E. pachystyla* (Clements 3588). 9. *E. pellucida* (Koyama 7012). Gap in bars = 1 μm . NCT = non-constricted tubercle, CT = constricted tubercle.



Figures 10-17. 10. *E. geniculata* (Godfrey 75703). 11-13. *E. melanocarpa* (Proctor 38072), 14. *E. quinquefolia* (Menapace 87). 15. *E. rostellata* (Hermann 4392). 16. *E. tenuis* (Hirt 1387). 17. *E. acicularis* (Mohlenbrock 5760). Gap in bars = 1 μ m.

son (1929), initially assigned *E. melanocarpa* to its own monotypic series, the *Melanocarpeae*. At the completion of his monographic study, however, Svenson (1939a) abandoned the *Melanocarpeae* relegating *E. melanocarpa* to uncertain status.

Later, Svenson (1957) again modified his view and formally delegated *E. melanocarpa* to the series *Pauciflorae*, although a detailed explanation regarding this assessment was not given.

As previously noted, the tubercles of *Pauciflorae* achenes are confluent with the achene body (Figure 2). There is little doubt that the highly appressed, non-constricted tubercle of *E. melanocarpa* (Figure 11) was a key factor in Svenson's decision to allocate *E. melanocarpa* to the *Pauciflorae*. Although the convolute anticlinal cell walls of *E. melanocarpa* (Figures 12 and 13) do not repudiate Svenson's decision to assign *E. melanocarpa* to the *Pauciflorae*, given the absence of achene conformity at the micro-morphological level within the *Pauciflorae* (e.g., *E. quinqueflora* (F. X. Hartm.) O. Schwarz, Figure 14, and *E. rostellata* Torr., Figure 15), the author questions whether the series, is in fact, a natural entity.

Similar to *E. albida*, the convolute anticlinal cell walls of *E. melanocarpa* implies a relationship with either the *Multicaules* or *Sulcatae*.

***Eleocharis minarum* Boeck.**

Eleocharis minarum is a taxon of questioned authenticity. Svenson (1939b), after examining the syntypes deposited at Stockholm (S) and Copenhagen (C), discovered that *E. minarum* was based on immature plants, possibly allied to *E. dunensis* Kuek. of the series *Sulcatae*. The author has also inspected the Stockholm and Copenhagen plants, and concurs with Svenson's assessment.

A thorough search of the world's major herbaria failed to secure a mature specimen of *E. minarum*. Given the absence of a plant bearing mature achenes, a micro-morphological evaluation was not possible.

***Eleocharis squamigera* Svens.**

This species is a South American spikerush about which little has been published. *Eleocharis squamigera* has been collected from scattered localities throughout the tropical regions of the continent (Svenson, 1934).

According to Svenson (1934), the general morphological appearance of *E. squamigera* is similar to *E. tenuis* Schult., of the

series *Palustriformes* subseries *Truncatae*. In fact, the type specimens of *E. squamigera* were initially assigned to *E. tenuis* (Svenson, 1934). Nonetheless, the micro-morphology of the achenes differ in that the anticlinal cell walls of *E. squamigera* (Figures 18 and 19) are crenate to serrate, while those of *E. tenuis* (Figure 16) are serrulate to entire. Furthermore, the cell lumens of *E. tenuis* are more concave than those of *E. squamigera*. Clearly, the two plants are distinct, allied taxa.

Svenson (1934) also suggested an affinity with the series *Aciculares*. However, achenes of the *Aciculares* possess highly elevated anticlinal cell walls (e.g., *E. acicularis* (L.) R. & S., Figure 17), a feature which is lacking from the achenes of *E. squamigera*.

Although the achene micro-morphology of *E. squamigera* contrasts somewhat with that of *E. tenuis*, it does approximate other taxa of the series *Palustriformes* subseries *Truncatae* (e.g., *E. nodulosa* (Roth) Schult., Figure 20, and *E. intermedia* (Muhl.) Schult., Figure 21).

***Eleocharis subarticulata* (Nees) Boeck.**

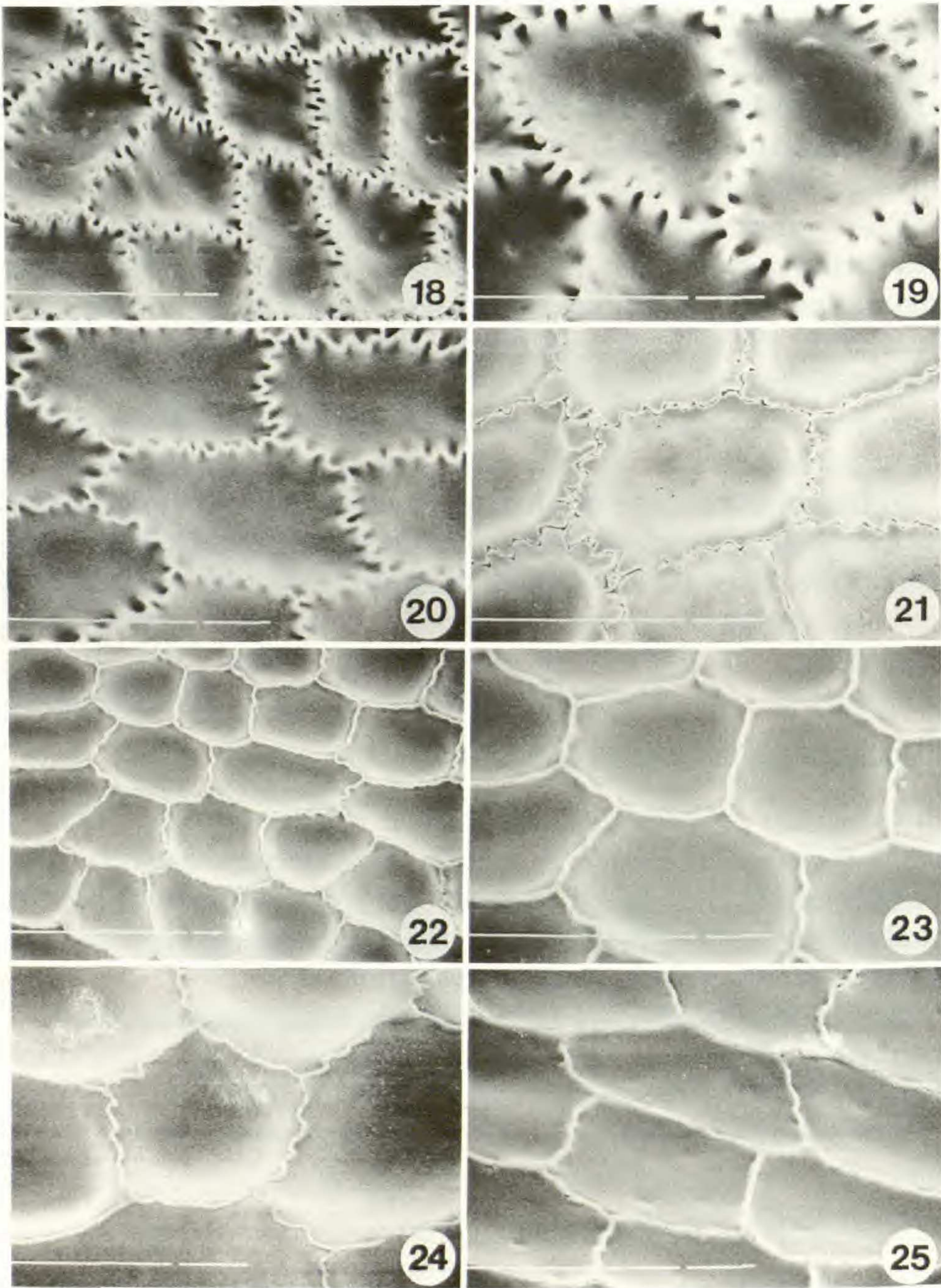
Eleocharis subarticulata, like much of the spikerush flora of Latin America, suffers from a lack of modern studies. Svenson (1939b) found the vegetative and achene characters to be near *E. intermedia*, a plant of the series *Palustriformes* subseries *Truncatae* of North American distribution.

The micro-morphology of the achene wall (Figures 22 and 23) also suggests an alliance with the *Truncatae*. The anticlinal cell walls are repand to crenate with slightly concave lumens, attributes which are consistent in outline with *E. elegans* (H.B.K.) R. & S. (Figure 24) and to a lesser extent with *E. elliptica* Kunth (Figure 25).

SUMMARY

Micro-morphological characters of the achene wall add credence to Svenson's (1929) conclusion that *E. albida* is allied to the series *Sulcatae*. The results are equally conducive, however, to a relationship with the series *Multicaules*. Consequently, a definitive decision regarding the serial placement of *E. albida* was not obtained.

The micro-morphological attributes affiliated with the achenes



Figures 18–25. 18 and 19. *E. squamigera* (Smith 13673). 20. *E. elegans* (Proctor 34808). 21. *E. intermedia* (Dickson 1413). 22 and 23. *E. subarticulata* (Smith 13673). 24. *E. nodulosa* (Proctor 25301). 25. *E. elliptica* (Menapace 24). Gaps in bar = 1 μ m.

of *E. melanocarpa* were also inconclusive. The convolute anticlinal cell walls suggest a kinship with either the *Multicaules* or *Sulcatae*. Nonetheless, the evidence is once again equivocal as to which series is in fact the best alternative.

Given the continued ambiguity surrounding the serial placement of *E. albida* and *E. melanocarpa*, it is considered best to retain their status as "species of uncertain classification."

With regard to *E. squamigera* and *E. subarticulata*, the author has concluded that the achene micro-morphology constitutes sufficient evidence, in conjunction with the overall macro-morphological affinities, to assign *E. squamigera* and *E. subarticulata* to the series *Palustriformes* subseries *Truncatae*.

An assessment of *E. minarum* proved to be impossible due to the absence of a specimen bearing mature achenes.

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